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ENTOMOPATHOGENIC FUNGI (ZYGOMYCOTINA: ENTOMOPHTHORALES) INFECTING CEREAL APHIDS (HOMOPTERA: APHIDIDAE) IN MONTANA

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Abstract.—A field survey of dryland and irrigated crops of small grains was conducted in Montana during the 1990 growing season to search for entomopathogenic fungi for use in the biological control of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko). Dryland crops were heavily infested by *D. noxia,* but no evidence of fungal infection was found among the populations of this aphid species. *Diuraphis noxia* populations were undetectable on spring grains grown under irrigation. However, other cereal aphids, mainly *Metopolophium dirhodum* (Walker) and *Rhopalosiphum maidis* (Fitch), occurred abundantly. Mycoses caused by Entomophthorales were observed killing both aphid species from late July through August. Among 292 aphid cadavers collected during the occurrence of mycoses, 45.9% were killed by *Pandora neoaphidis* (Remaudière & Hennebert) Humber, 31.8% by *Conidiobolus obscurus* (Hall & Dunn) Remaudière & Keller, 21.6% by *Entomophthora planchoniana* Cornu, and 0.7% by *Zoophthora radicans* (Brefeld) Batko. Among the aphids killed by *C. obscurus,* the proportion of cadavers producing resting spores inside the body, rather than primary conidia on the body surface, increased quickly as the incidence of infection decreased on both aphid hosts. Distinguishing features of the two true *Entomophthora* species, *E. planchoniana* and *E. chromaphidis* Burger & Swain, infecting aphids in North America are discussed in comparison with information reported from different geographic areas. The four fungal species, plus *Conidiobolus thromboides* Drechsler, which was not found in 1990, but was successfully isolated from *Diuraphis tritici* (Gillette) in 1989, are new records as pathogens of cereal aphids for Montana.

Key Words.—Insecta, cereal aphids, Aphididae, Entomophthorales, aphid-pathogenic fungi, biological control agents

Aphids are often subject to attack by entomopathogenic fungi, including numerous species of Entomophthorales (Latgé & Papierok 1988, Waterhouse & Brady 1982) and at least two species of Hyphomycetes (Feng & Johnson 1990; Feng et al. 1990a, b; Hall 1981). These fungi are considered to have great potential as candidates for use in microbial control of various aphids (Latgé & Papierok 1988).

Fungal pathogens infecting cereal aphids have been reported in Europe (Dean & Wilding 1971, 1973; Dedryver 1983; Papierok & Havukkala 1986) and South America (Lássari 1985). Some regional lists of aphid fungi have also been published in Australia (Milner et al. 1980), Finland (Papierok 1989) and Israel (Ben-Ze'ev et al. 1984). In North America, five entomophthoralean species have been recorded from 34 aphid host species in the eastern United States and Canada

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(Remaudière et al. 1978). Recently, Feng et al. (1990b) recovered 10 species of fungal pathogens from several species of cereal aphids infesting grain crops grown under irrigation in southwestern Idaho. One of these aphid hosts is the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), a recently-introduced, devastating pest of small grains in North America (Burton 1988). Microbial control, involving the use of entomopathogenic fungi, is one promising strategy that will contribute to the management of this pest in the future (Burton 1988, 1989).

This study surveyed for fungal pathogens of cereal aphids in dryland and irrigated small grains in Montana and generate regional strains for use in both laboratory and field studies.

Materials and Methods

Field Survey.—A field survey conducted in Montana during the 1990 growing season included dryland and irrigated crops. The dryland crops were fall-sown winter wheat in two fields and spring-sown barley in one field located 25 or 35 km west of Billings. The irrigated crops were several small experimental plots of late-sown spring wheat and barley on the Montana State University campus in Bozeman. The survey was initiated in mid-May and continued through harvest. The fields were visited each week.

On each field date, numerous aphid colonies throughout each of the fields were examined carefully to determine if any aphids were infected with fungal pathogens. On the dryland crops, this examination was made while samples, ranging from 100 to 960 tillers (decreasing with increasing aphid density), were randomly taken in each field for purposes of estimating aphid population levels. Aphid cadavers, when found in the colonies, were placed in plastic vials in a cooler and transported to the laboratory for identification and isolation of fungal agents responsible for aphid mortality.

Identification of Aphid-Pathogenic Fungi.—External symptoms and fungal reproductive structures from each of the aphid cadavers were examined under a dissecting microscope as soon as possible following the collection (within the same day). Desiccated specimens were maintained in a moist chamber for several hours to allow for development of reproductive structures. Cadavers were then individually mounted on glass slides using cotton blue or aceto-orcein stains. Identification was based on external symptoms and the morphology of spores and sporulating structures (Waterhouse & Brady 1982). A recent revision of the classification for the Entomophthorales (Humber 1989) was used. The fungi associated with the cadavers were considered to have caused the death of their hosts if they had been previously documented as pathogens of aphids in the literature.

Isolation of Aphid-Pathogenic Fungi.—Saubouraud dextrose agar (DIFCO Laboratories, Detroit, Mich.) supplemented with 1% yeast extract (DIFCO, Laboratories, Detroit, Mich.) was used as a basic medium (SDAY) to isolate fungal pathogens from infected aphids. Some fresh aphid cadavers were individually attached to a small piece of double-faced sticky film in the center of a Petri dish cover. Cadavers were suspended over SDAY medium in the bottom of a Petri dish for a period of 10–20 h and then removed. Discharged spores from the cadaver would thus fall down to the medium for initiation of an in vitro culture. The Petri dishes containing inoculum were incubated at approximately 20° C with a photoperiod of 16:8 (L:D).

Results and Discussion

The dryland crops were heavily infested by *D. noxia* during the 1990 growing season. Mean population densities (± SE) on average reached 14.4 (± 46.5) and 47.9 (± 87.4) aphids per tiller in the two winter wheat fields, respectively and 136.2 (± 102.9) on the spring barley. The percentage of tillers infested was 50%, 86%, and 96%, respectively. Other cereal aphids were occasionally found, but no consistent populations were detected. Despite the high levels of *D. noxia* populations on the dryland crops, no aphids were found to be infected by any fungal pathogens during the growing season.

Diuraphis noxia populations were undetectable on regularly sown grain crops in the Bozeman area during the growing season. However, other cereal aphids, including the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), and the rose-grass aphid, *Metopolophium dirhodum* (Walker), occurred abundantly in the small plots of late-sown spring grains grown under irrigation after early July. Mycoses induced by entomophthoralean fungi were observed killing both aphid species from late July through late August.

Four species of entomophthoralean fungi were identified from among the 292 cadavers of *M. dirhodum* and *R. maidis* collected during the four-week period of mycosis development. Nearly half of those cadavers (45.9%) were killed by *Pandora neoaphidis* (Remaudière & Hennebert) Humber, 31.8% by *Conidiobolus obscurus* (Hall & Dunn) Remaudière & Keller, 21.6% by *Entomophthora planchoniana* Cornu, and 0.7% by *Zoophthora radicans* (Brefeld) Batko. The identity and descriptions of these fungi are given separately below.

Conidiobolus *spp.*—Although only a single species, *C. obscurus,* was found among the *Conidiobolus*-killed aphids in the 1990 growing season, another fungus, *Conidiobolus thromboides* Drechsler, was successfully isolated from an infected individual of the western wheat aphid, *Diuraphis tritici* (Gillette), on winter wheat in Bozeman during the fall of 1989. Hence, these two species are listed here together as Montana records. *Conidiobolus obscurus* was recovered from 30 *M. dirhodum* and 63 *R. maidis* cadavers. Several isolates of *C. obscurus* have been obtained from both aphid hosts on SDAY and sent to ARSEF (USDA-ARS Collection of Entomopathogenic Fungal Cultures, USDA-ARS Plant Protection Research Unit, U.S. Plant, Soil and Nutrition Laboratory, Ithaca, New York) for permanent storage.

Aphids recently killed by *C. obscurus* were grey or grey-brown, and were attached to the plant by their probosces. Neither rhizoids nor cystidia were present. Conidiophores were simple, unbranched (Fig. 1a). Primary conidia containing many globules were nearly spherical (Fig. 1b), and measured as 33.8 (28.8–37.5) × 28.0 (22.5–33.8) μm ($n = 100$). Secondary conidia formed from primary conidia by germination (Fig. 1c). Resting spores (Fig. 1d) were spherical with a diameter of 36.5 (27.5–45.0) × 35.4 (27.5–43.8) μm ($n = 50$). No differences were significant in the dimensions of the primary conidia ($t_1 = 1.41$, $P > 0.10$; $t_2 = 0.53$, $P > 0.50$; df = 98) and resting spores ($t_1 = 1.10$, $P > 0.20$; $t_2 = 0.50$, $P > 0.50$; df = 98) between the two aphid hosts. However, the primary conidia [39.6 (28.8–33.7) × 33.7 (25.0–44.3) μm, $n = 50$] and resting spores [38.9 (36.3–43.8) × 37.4 (35.0–40.0) μm, $n = 15$] from in vitro cultures were significantly larger than the primary conidia ($t_1 = 10.03$, $P < 0.01$; $t_2 = 11.09$, $P < 0.01$; df = 148) and resting spores ($t_1 = 4.55$, $P < 0.01$; $t_2 = 3.74$, $P < 0.01$; df = 113) collected in vivo, respectively.

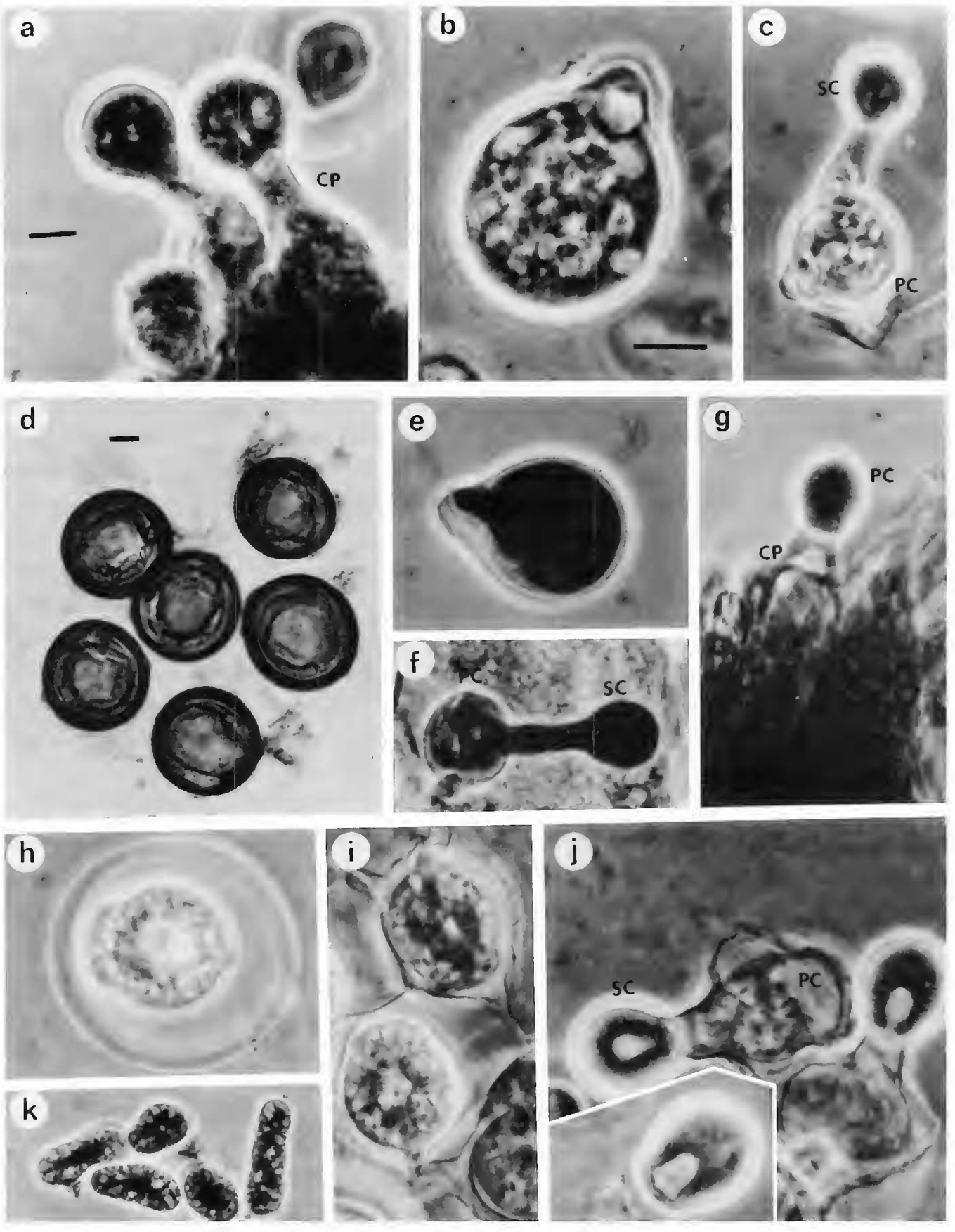

Figure 1. (a–d) *Conidiobolus obscurus,* (e–f) *C. thromboides,* and (g–k) *Entomophthora planchoniana.* (a) Developing conidiophores (CP). (b) A primary conidium. (c) A secondary conidium (SC) being produced from a primary conidium (PC). (d) Resting spores of *C. obscurus.* (e) A primary conidium. (f) A secondary conidium (SC) being produced from a primary conidium (PC) of *C. thromboides.* (g) A conidiophore. (h–i) Primary conidia imbedded in cytoplasms. (j) Secondary conidia (SC) being produced from primary conidia (PC). (k) Hyphal bodies germinated from conidia of *E. planchoniana.* Scale bars: 10 μm. The bar on (a) applies to (c) and (g); the bar on (b) applies to (e), (h–j); and the bar on (d) applies to (k).

The primary conidia of *C. thromboides* were subspherical, but smaller (Fig. 1e) than those of *C. obscurus.* The measurements from the in vitro culture were 26.4 (22.0–31.3) × 20.9 (17.5–23.8) μm (n = 50). The resting spores were also similar in shape but smaller than those of *C. obscurus.*

Entomophthora planchoniana.—This fungus was recovered from 37 *M. dirhodum* and 26 *R. maidis* cadavers. No attempt was made to obtain a pure culture because true *E. planchoniana* has rarely been successfully cultured using an artificial medium.

Aphids killed by *E. planchoniana* were yellow-brown or brick brown and stuck to the plant by rhizoids in a thick bundle or several bundles forming a platform. Cystidia were absent. Conidiophores were unbranched (Fig. 1g). Primary conidia were typically discharged with a mass of cytoplasm creating a 'halo' (Fig. 1h, 1i). Primary conidia were bell-shaped and measured as 18.9 (15.0–22.5) × 15.5 (12.0–17.8) μm ($n = 75$). Secondary conidia (Fig. 1j) that germinated from the primary conidia were more rounded and smaller than the primary conidia: 15.1 (13.3–17.5) × 12.6 (10.8–14.8) μm ($n = 50$). No resting spores were observed from the materials examined.

There are only two true *Entomophthora* species that have been documented as aphid pathogens in the world: *E. planchoniana* and *E. chromaphidis* Burger & Swain. *Entomophthora planchoniana* is well known in Europe (Waterhouse & Brady 1982; Papierok 1989) and also has been reported in Israel (Ben-Ze'ev et al. 1984) and Australia (Milner et al. 1980). In North America, however, this species has been recorded only from two aphid cadavers of unknown identity that were collected from the eastern coast (Remaudière et al. 1978). On the other hand, *E. chromaphidis* was originally described from the walnut aphid, *Chromaphidis juglandicola* (Kaltenbach), in southern California (Burger & Swain 1918) and recently recovered from cereal aphids in southwestern Idaho (Feng 1990). The two species can be distinguished from each other by the size of primary conidia and the number of nuclei in each conidium (R. A. Humber, MGF, unpublished data). Primary conidia of *E. chromaphidis* contain 2–8 nuclei each and are generally smaller than those of *E. planchoniana,* which contain 2–6 nuclei (Waterhouse & Brady 1982). There was no significant difference in the size of the primary conidia from *M. dirhodum* and *R. maidis* cadavers, killed by *Entomophthora* in Montana, compared to those seen in other reports (Table 1) from Europe and Australia. However, the primary conidia of the *Entomophthora* from Montana are significantly larger than those of the real *Entomophthora* species reported from California and Idaho. The comparison did not include the materials from Israel (Ben-Ze'ev et al. 1984) and the east coast of North America (Remaudière et al. 1978) because the authors did not provide measurements. Unfortunately, our specimens were not stained well enough to allow the counting of the nuclei inside the conidia because almost all the primary conidia were imbedded in the cytoplasm. Even so, the Montana fungus could be *E. planchoniana* rather than *E. chromaphidis* because of the similarity to the European fungus in conidial size.

Pandora neoaphidis.—A total of 134 cadavers, including 115 *M. dirhodum* and 19 *R. maidis,* were attributed to infection by *P. neoaphidis.* No isolates were obtained using SDAY.

Aphids freshly killed by *P. neoaphidis* turned pale brown or yellow-brown and adhered to the plant by numerous rhizoids, each of which consisted of a thin stalk ending in a disk-like terminal expansion. Cystidia, present under moist conditions, were distally tapered, thicker than conidiophores, and extended far beyond them (Fig. 2a). Conidiophores were digitately branched at their apices (Figs. 2a, 2b). Primary conidia contained a single large nucleus, were ovoid to cylindrical in

Table 1. Comparison of the sizes of primary conidia of true *Entomophthora* species from aphids in Montana and other geographic areas.

Region	Fungus[a]	Primary conidia, μm L/W[b]	Mean[c]	Range	t[d]	P	Reference
Australia	*Epl*	L	(17.0)	14–20	1.61	>0.10	Milner et al. 1980
		W	(15.0)	13–18	0.47	>0.50	
England	*Epl*	L	19.0	14–23	−0.09	>0.50	Waterhouse & Brady 1982
		W	14.0	12–20	1.32	>0.10	
Finland	*Epl*	L	18.1	13–22	0.68	>0.40	Papierok 1989
		W	14.9	10–18	0.55	>0.50	
California	*Ech*	L	(12.5)	11–14	5.42	<0.01	Burger & Swain 1918
		W	(10.5)	10–11	4.33	<0.01	
Idaho	*Ech*	L	14.4	13–16	3.79	<0.01	Feng 1990
		W	12.3	10–13	2.82	<0.01	

[a] *Epl* = *E. planchoniana, Ech* = *E. chromaphidis.*

[b] L = length (including papillae), W = width.

[c] Table entries in brackets estimated from the range of original measurements but not given directly by the authors.

[d] t-test under null hypothesis H_0: $x_{MT} = y_{COM}$, where x_{MT} is the measurement from Montana material (L: 18.89 ± 1.17; W: 15.54 ± 1.16; $n = 75$), Y_{COM} the measurement from the materials compared, and $t = (x_{MT} - y_{COM})/SE_x[(n + 1)/n]^{1/2}$ with df = $n - 1$.

shape (Fig. 2c) and measured 23.6 (18.8–30.0) × 12.4 (10.0–15.0) μm ($n = 80$). Secondary conidia developed from primary conidia (Fig. 2d) and were similar in shape but smaller than the primary conidia. No resting spores were present in the specimens examined.

Zoophthora radicans.—This fungus was recovered from two *M. dirhodum* cadavers only. Because of the paucity of specimens, no attempt was made to isolate *Z. radicans,* although it usually grows quite well on SDAY.

Aphids killed by *Z. radicans* were pale brown or orange-brown. Rhizoids were present. Cystidia were also present, but were relatively few in number compared with those of *P. neoaphidis.* Conidiophores were branched (Fig. 2e). Primary conidia were uninucleate, long and ellipsoid in shape (Fig. 2f): 18.3 (15.3–21.3) × 7.4 (6.5–8.8) μm ($n = 50$). Secondary conidia germinated apically or laterally from primary conidia and were similar to primary conidia. No capilliconidia and resting spores were observed in the limited number of specimens.

Development of Aphid Mycosis.—The relative proportion of infections by *P. neoaphidis* tended to increase during the 4 week period of mycosis development, whereas that of *C. obscurus* appeared to decrease (Fig. 3). The fungus, *Z. radicans,* was observed only at the beginning of the period. Thereafter, it remained undetected or possibly its influence on the aphids was masked by other fungi. The infection by *E. planchoniana* remained about the same among the aphids after early August (Fig. 3). More *M. dirhdodum* cadavers were attributed to infection by *P. neoaphidis* than were *R. maidis* cadavers. The reverse was true for *C. obscurus.*

Many of the aphids killed by *C. obscurus* produced resting spores rather than primary conidia, which are the primary form infecting live aphids. As shown in Fig. 4, the proportion of cadavers containing resting spores in the field appeared to increase during the 4 week period, irrespective of the species of aphid host.

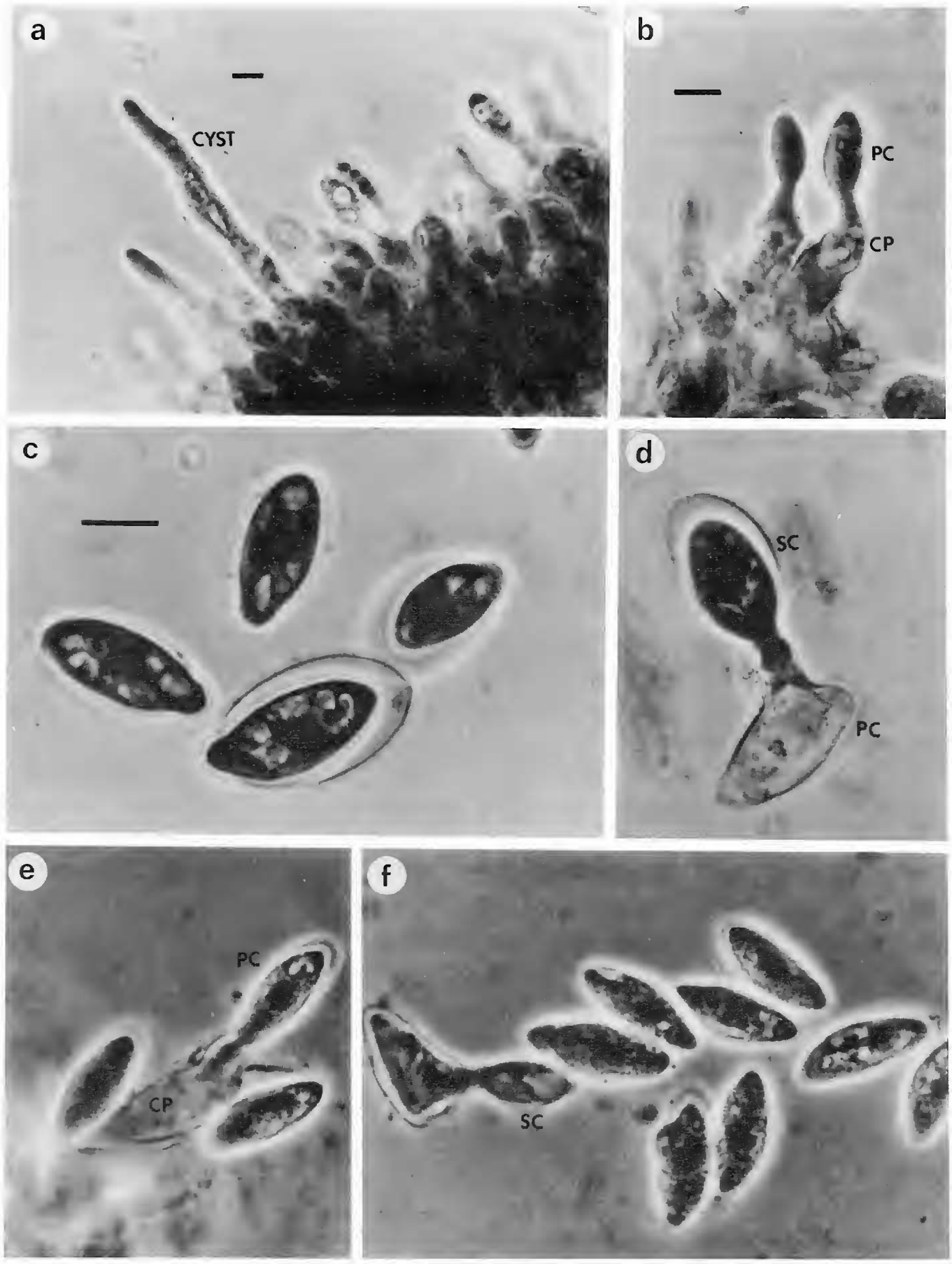

Figure 2. (a–d) *Pandora neoaphidis* and (e–f) *Zoophthora radicans*. (a) Cystidia (CYST). (b) Conidiophores. (c) Primary conidia. (d) A secondary conidium (SC) being produced from a primary conidium (PC). (e) Conidiophores. (f) Primary conidia and secondary conidium (SC). Scale bars: 10 μm. The bar on (c) applies to (d–f).

This phenomenon has not been reported by previous researchers (e.g., Feng et al. 1990b, Milner et al. 1980, Papierok 1989) although resting spores of *Conidiobolus* spp. from aphids are frequently observed from in vitro cultures. The production of resting spores is often thought to require a short photoperiod or low temperature or a combination of both for initiation (Wilding & Latteur 1987). However, during

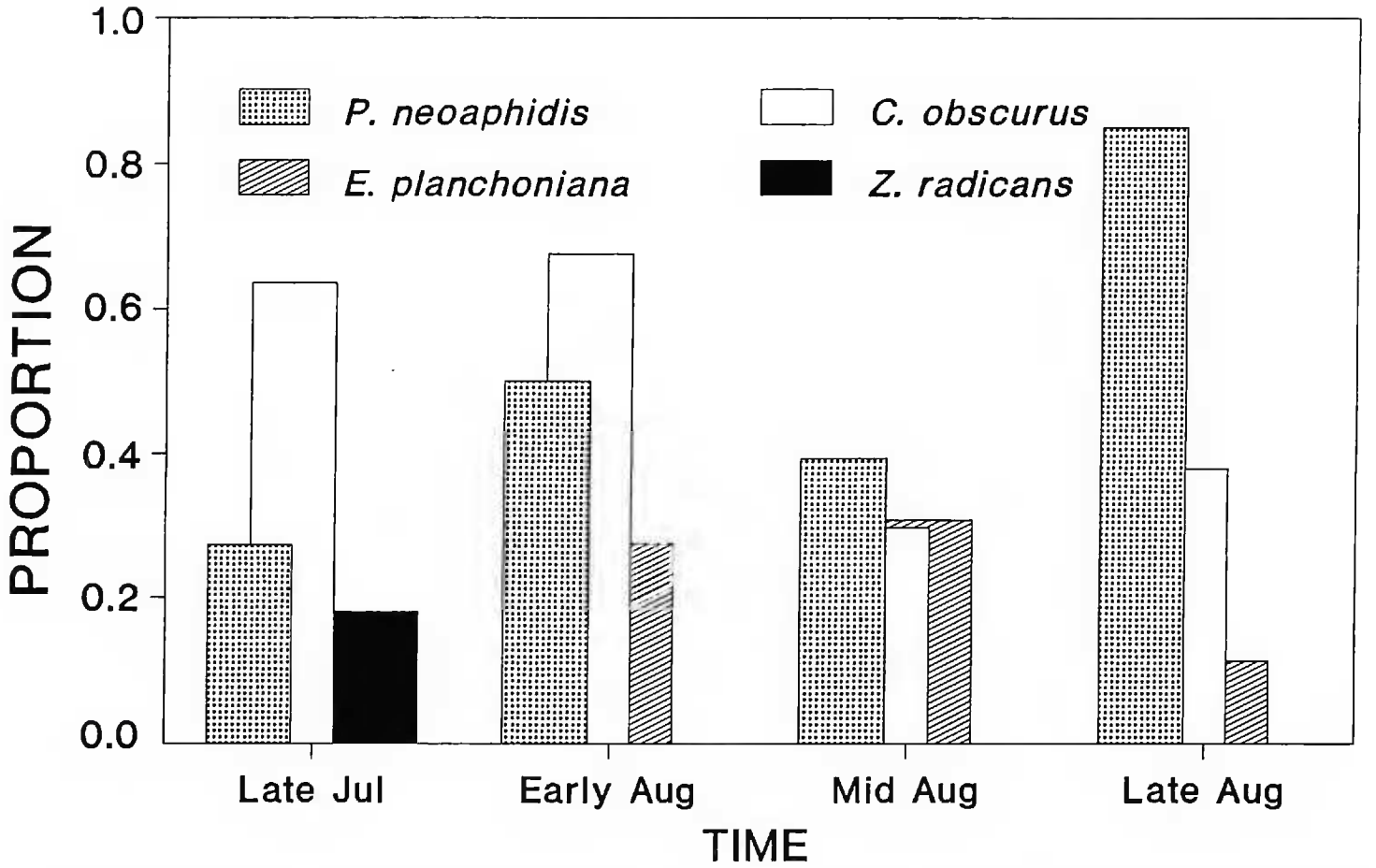

Figure 3. Proportion of each fungal pathogen among the cadavers of *M. dirhodum* and *R. maidis* in irrigated spring grains in Bozeman, Montana during the 1990 growing season.

the period from late July to late August in 1990, the natural photoperiod and temperature in Bozeman remained in a summer pattern: 14–15 h day length and mild temperature conditions; the monthly mean temperature for August was 19.4° C (11.0–27.9° C). It is unclear whether any other environmental factors may have been involved in this phenomenon.

The production of resting spores in the field implies an interruption of the fungal infection cycle, because generally following resting spore formation a minimum period of vernalization is required before germination is initiated (Wilding & Latteur 1987). This may explain why the level of infection by *C. obscurus* decreased among the aphids during the survey (Fig. 3). This also suggests that for *Conidiobolus* species to be successfully used against cereal aphids in Montana, additional understanding of the mechanisms for the production and germination of resting spores will be required.

The mortality of cereal aphids resulting from fungal infection in Bozeman was at low levels (< 10%) compared with those reported from cereal aphids in irrigated spring wheat in southwestern Idaho (up to 90%; Feng 1990). The frequent thundershowers from late July through early August as well as the irrigation water provided may have enhanced the development of fungal infection in the aphid populations in Bozeman. Arid weather (low moisture and high temperature) may have prevented fungal diseases from developing in the aphid populations on dryland crops.

The four species of Entomophthorales, found during the 1990 season, plus the *C. thromboides* isolate, obtained in the fall of 1989, are new records as pathogens of cereal aphids for Montana. *Entomophthora planchoniana* represents the first record from cereal aphids in North America.

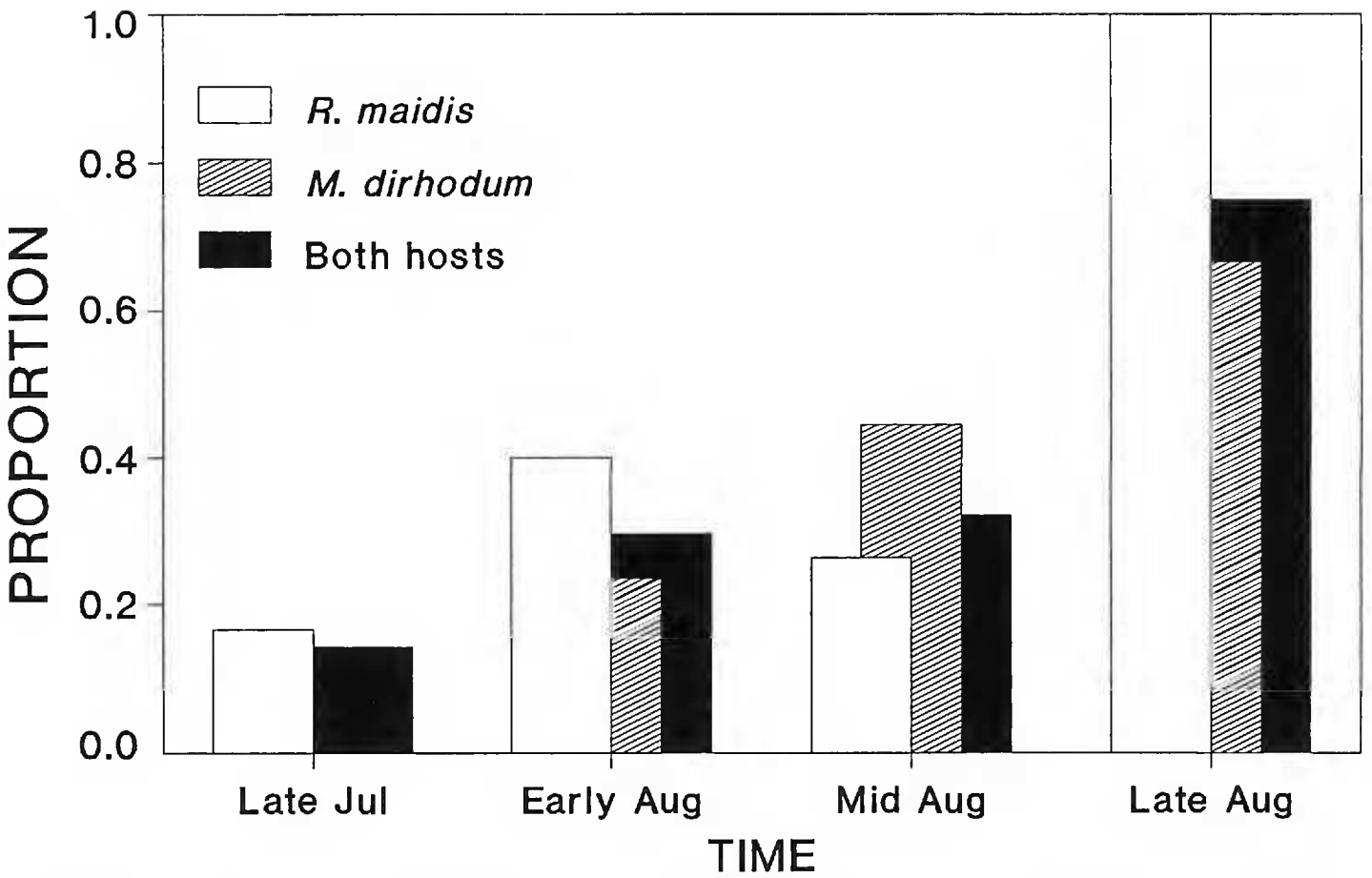

Figure 4. Proportion of aphid cadavers producing resting spores in irrigated spring grains in Bozeman, Montana during the development of mycosis.

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